Laboratory and Realized Host Ranges of *Chaetorellia succinea* (Diptera: Tephritidae), an Unintentionally Introduced Natural Enemy of Yellow Starthistle

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ABSTRACT In 1999, we reported our discovery, in California and Oregon, of *Chaetorellia succinea* (Costa) (Diptera: Tephritidae) destroying the seeds of yellow starthistle, *Centaurea solstitialis* L., one of the worst weeds in the western United States. This fly, an unintentional introduction from Greece, dispersed rapidly throughout California and the northwest, and there is interest in using this adventive fly as a classical biological control agent for this weed. Because the host range of *Ch. succinea* has not been studied, this fly might pose a risk to other members of the thistle tribe Cardueae, especially the many thistle species native to California and other parts of the western United States. We determined the physiological host range of this fly in the laboratory by exposing it under no-choice conditions to 14 potential Cardueae hosts. Two introduced weed species and the native American basketflower (*Centaurea americana* Nuttall) were laboratory hosts. Under less restrictive choice test conditions, yellow starthistle was highly preferred, but there was a small amount of oviposition, and a few adult *Ch. succinea* emerged from all three of these plant species. Because *Ch. succinea* is now widespread throughout California, we collected flower heads from 24 potential host plant species at 111 sites to determine the realized host range in the field. These collections did not include American basketflower, which does not occur naturally in California. *Ch. succinea* emerged only from the other two known hosts: *Ce. melitensis* and *Ce. sulfurea*. Our results suggest that American basketflower growing in the southwestern United States may be at risk if *Ch. succinea* expands its range into that region.

KEY WORDS biological control of weeds, nontarget impact, *Centaurea solstitialis*, *Cirsium* species, stepping-stone host

Yellow starthistle (*Centaurea solstitialis* L.), an invasive weed native to the eastern Mediterranean, western Asia, and northern Africa, is now established in at least 41 United States (USDA–NCRS 2006) and across the southern portion of Canada. Yellow starthistle is most widespread and damaging in California and the Pacific Northwest. The inflorescences, technically called "capitula" but hereafter referred to as "heads," are surrounded by long spines that deter feeding by cattle and limit or prevent recreational use within infested areas. Yellow starthistle displaces native vegetation and reduces biodiversity, and it can cause a fatal neurological disease if ingested by horses (Cordy 1978, Fuller and McClintock 1986). Overseas surveys and research to locate potential biological control agents for yellow starthistle began in the late 1950s (Balciunas 1998) and eventually led to the release of six insects, all of which attack yellow starthistle heads and destroy or inhibit developing seeds (Ehler and Andres 1983, Turner et al. 1995, Pitcairn et al. 1998).

During our 1995 and 1996 surveys to document the establishment and distribution of one of these agents, the fly *Chaetorellia australis* Hering (Diptera: Tephritidae), we detected the presence of another, very similar fly, eventually identified as *Ch. succinea* (Costa) (Balciunas and Villegas 1999). By examining voucher specimens at the quarantine facility in Albany, CA, and those held by cooperators who had assisted in the early releases of *Ch. australis*, we determined that the most probable source of the United States introduction of *Ch. succinea* was a 1991 shipment of yellow starthistle heads from Greece that contained both *Chaetorellia* spp. Flies from this shipment were released at a site near Merlin, OR, and both species established there. *Ch. succinea*, but not *Ch. australis*, dispersed rapidly, and the former can now be expected at nearly every yellow starthistle site in California (Balciunas and Villegas 1999, Pitcairn et al.

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2003) and is spreading its range in Idaho, Nevada, Oregon, and Washington (J.K.B., unpublished data).

Chaetorellia spp. females oviposit on the developing heads of plants in the tribe Cardueae of the plant family Asteraceae. The eggs of both *Ch. australis* and *Ch. succinea* are deposited on the outside of the developing heads, and the emerging neonates burrow into the heads, and the larvae feed within a single head on receptacle tissue and on the developing seeds (White and Marquardt 1989, J.K.B., unpublished data). Because *Ch. succinea* is widespread and destroys many yellow starthistle seeds, some people advocate its use as a biological control agent. However, the host range of this fly has not been studied sufficiently to predict nontarget impacts, so deliberate additional introductions might be considered as unethical (Delfosse 2005).

After detecting this new *Chaetorellia* in mid-1996, we immediately curtailed further releases of *Chaetorellia* spp. and began studying the safety of *Ch. succinea.* Earlier, we showed that this fly presents only a small risk to safflower (*Carthamus tinctorius* L.) growers in California (Balciunas and Villegas 2001). However, we have also been concerned that this fly might attack native species related to yellow starthistle. In addition, we did not know if this fly might have alternate hosts among the many introduced Cardueae thistles and knapweeds. In this paper, we present the results of field and laboratory studies to determine other possible hosts for this fly. In the laboratory, we determined the acceptability of various plants in this tribe for oviposition and development of *Ch. succinea.* We also collected potential Cardueae hosts in the field and examined them for evidence of attack by *Ch. succinea.*

Materials and Methods

We distinguished adults of *Ch. succinea* from other *Chaetorellia* spp. by the presence of an extra one or two spots on the posterior dorsolateral portion of the thorax. White and Marquardt (1989) placed the nine known species of *Chaetorellia* into two groups, with *Ch. succinea* belonging to the *Ch. loricata* group and *Ch. australis* to the *Ch. jaceae* group. *Ch. succinea* adults (and the other two species of the *Ch. loricata* group) have one (sometimes two) additional spots on the posterior dorsolateral portion of each side of their thoraxes, leading to an aggregate of 10 (sometimes 12) spots on the entire thorax. These additional spots are lacking in *Ch. australis* and the other five species in its group that have only eight spots on the thorax. Because no other members of the *Ch. loricata* group have been recorded in North America, we use these extra spots as an easy way to distinguish *Ch. succinea* from all other *Chaetorellia* flies found here. We deposited voucher specimens of our *Ch. succinea* in the United States National Museum at the Smithsonian in Washington, DC, and in the California State Collection of Arthropods in Sacramento, CA.

For the host plants, we continue to follow the widely used terminology and assignments of the Asteraceae tribe and subtribe classifications as applied by Bremer (1994), although newer classifications (Garcia-Jacas et al. 2002) have been proposed. The large genus *Centaurea* is considered polyphyletic, and there have been quite a few proposed shifts of species into other genera (Garcia-Jacas et al. 2000, 2001), but we use only those that are reflected in the web-based PLANTS Database (USDA–NCRS 2006). For common names of weeds, we use those in the "Composite List of Weeds" (WSSA 1989), and for common names of the native plants, we follow Hickman (1993).

Laboratory Tests. We conducted laboratory evaluations of the acceptability of different Cardueae as hosts for *Ch. succinea* at the USDA–ARS quarantine laboratory in Albany, CA. These laboratory tests began in 1999 and continued through 2004. We used newly emerged adults exiting from yellow starthistle heads collected at our study sites in California and Nevada. *Chaetorellia* will oviposit only on flower heads at the appropriate stage of development (buds still closed, but approximately a week before anthesis). Using the flower stage designations of Maddox (1981), the heads of the test plants and yellow starthistle controls used in our tests were Bu-3s and Bu-4s. Under laboratory conditions, it is frequently difficult to induce bolting and flowering by some Cardueae, especially the native *Cirsium* thistles. The combination of test plants at the appropriate flowering stage and of adequate numbers of newly emerged *Ch. succinea* was difficult to synchronize and occurred only a few times each year. Therefore, many years were needed to complete the array of laboratory tests.

Depending on the size of the test plant, we used either wooden and glass cages (73 by 42 by 49 cm) or metal screen cages (122 by 91 by 91 cm) for the laboratory host range tests. In no-choice tests, the flies (n = 3–12 male-female pairs) were exposed to one to three test plants of the same species in the cage. These no-choice tests had two phases: a no-choice phase and a sequential control phase. To verify that the females were indeed fertile, after 2–3 wk, the surviving flies were transferred to another cage with yellow starthistle control for a similar period of time. The flies were removed, and the test plants and yellow starthistle controls kept in separate cages for at least another 3 wk to allow any *Ch. succinea* larvae to complete development and emerge as adults. The heads from the test plants and yellow starthistle controls were cut off the plants and held for an additional 3–4 wk in emergence boxes to allow for late-emerging flies. Emergence boxes were closed cardboard boxes (either 36 by 36 by 36 cm or 32 by 24 by 36 cm) with a clear vial partially inserted into one side. Approximately 4 wk later, after flies ceased emerging in the boxes, we dissected all the heads of both the test plants and the yellow starthistle controls. The contents of each head were examined, and we considered a head as infested or damaged if we could detect larval feeding damage, an empty pupal case, or a dead or overwintering larva. Dead larvae were very uncommon (1–2% of the heads). Multiple larvae in one head were counted as one infested head.

If damage was detected to a test plant species during the no-choice tests, this species was evaluated further under choice conditions. The choice tests, conducted during 2001–2002, were similar to the no-choice tests, except that the flies (n = 4–6 pairs) were simultaneously exposed to the yellow starthistle control in the same cage with the test plant.

We tried to replicate each choice and no-choice test at least three times, but this was not always possible. Most of the test plants are biennials, sufficient bolting plants were not produced during the 5-yr test period, and some tests were discarded because of lack of oviposition on the yellow starthistle controls. For both the no-choice and the choice tests, we compared the ratio of infested heads on each test plant species against those for paired yellow starthistle control using Fisher exact test (Statistix 2005).

Field Evaluations. To locate potential collection sites, especially for native *Cirsium* spp. thistles, we contacted herbaria for specimen collection data and consulted with botanists and other colleagues. We found many of the introduced weedy species (*Centaurea, Cnicus, Silybum*) along roadsides or by consulting with County Agricultural Agents or others knowledgeable with local flora. Field collections began in 1998 and continued through 2001. Most of our collections were in California, but a few were from Oregon.

We attempted to collect at least 10 plants at each site, after flowering was nearly complete. Because we did not wish to endanger native plant populations, at any one site, we did not collect >10% of the individuals of a native species. Local populations of native thistles were frequently small, so we collected <10 plants at these sites. The number of plants and number of heads on each plant were usually recorded, and the heads were cut off and held in emergence boxes for up to 1 yr. Insects that emerged were collected, and the tephritid flies were identified. If *Chaetorellia* emerged from a sample, we would dissect at least a portion of the heads to determine infestation rates.

Results

Laboratory Tests. Between 1999 and 2004, we set up 53 no-choice tests, but only 29 were successful. We excluded 24 no-choice tests as unsuccessful because all the female *Ch. succinea* died before we could confirm their ovipositional status on the sequential yellow starthistle control; because the surviving females failed to oviposit on the yellow starthistle; or because we did not have a yellow starthistle plant in the appropriate bud stage to use as a control. We did, however, examine the test plants from these failed tests, and in no case was there any sign of oviposition or development by *Ch. succinea.* In two tests, although all the female flies were dead before the control phase, we did detect oviposition on the test plant. Both of these are included among the 29 successful tests.

Table 1 lists the results of the successful tests in which there was oviposition by *Ch. succinea*—eight species of *Centaurea,* four species of *Cirsium, Carthamus lanatus* L. ssp. *baeticus* (Boissier and Reuter) Nyman, and *Silybum marianum* L. Gaertner. All—except the four *Cirsium* species and *Ce. americana* Nuttall and *Ce. rothrockii* Greenman—are alien, introduced species, some of which are widespread and serious weeds. Of the 14 plant species we successfully tested, there was no evidence of oviposition by *Ch. succinea* on any *Cirsium* spp, the *Carthamus,* or the *Silybum.* However, three species of *Centaurea*: *Ce. americana* (American basketflower), *Ce. melitensis* (Maltese starthistle), and *Ce. sulfurea* (Sicilian starthistle), were attacked by this fly under no-choice conditions. Each of these three *Centaurea* species had three successful no-choice tests, and *Ch. succinea* emerged from all but one test on American basketflower and one test on Sicilian starthistle. The infestation rates in six of the seven tests in which the test plants showed oviposition were not statistically different compared with their paired, sequential yellow starthistle control. In addition, more than a dozen other tests in which no flies emerged were also statistically different from their yellow starthistle controls. Fisher exact test, like other analyses, is sensitive to low counts, and the variability among the number of heads among the species and within species, hindered reliable detection of statistical significance. Even when we pooled the results of the replicates for each species and compared them against the pooled counts for the yellow starthistle controls, the statistical analyses were not more reliable. Therefore, we do not further discuss statistical differences, including those in Table 2.

Biologically, any attack on a nontarget species by a candidate agent is important, even if statistical analyses fail to confirm it. Therefore, all three test plant species attacked in no-choice tests were further tested under choice conditions, with four to five replicates for each species (Table 2). Even under choice conditions, three of five tests of *Ce. americana,* three of four tests of *Ce. melitensis,* and one of five *Ce. sulfurea* tests had successful oviposition and development by *Ch. succinea.*

Field Evaluations. During 1996–2000, we made 111 field collections of mature plants in the Cardueae tribe (Table 3). Except for 10 collections from southern Oregon, all were from field sites in California. The majority (n = 84) were of 19 species/varieties of *Cirsium* thistles, with the remainder—except for one collection of *Cnicus benedictus* L.—being made up of four species of *Centaurea.* None of the *Cirsium* species or *Cnicus* produced any *Ch. succinea* or showed signs of fly attack. We made 10 collections of yellow starthistle growing in 10 California counties. We did not find this fly at our southernmost yellow starthistle site, near San Diego, but elsewhere it was present at densities ranging from 16 to 70% of the yellow starthistle heads at each site. *Ch. succinea* emerged from two of the three field collections of Malta thistle (*Ce. melitensis*) and from our single collection of Sicilian thistle (*Ce. sulfurea* Willdenow) but usually at lower densities (4–21%). As predicted by our laboratory tests, we did not recover any *Ch. succinea* from our 11 collections of cornflower (*Ce. cyanus* L.).

Table 1. Number of heads infested by *Ch. succinea* in each no-choice test consisting of a test plant species and its sequential yellow starthistle control

Test		Test plant				Yellow starthistle control			
Test no.	Test duration (days)	Females (*n*)	Species	Total heads	Heads with *Ch. succinea*	Females	Total heads	Heads with *Ch. succinea*	*P* value
CH-26–99	22	5	*Carthamus lanatus* L. ssp. *baeticus* (Boissier and Reuter) Nyman[a]	8	0	4	15	10	<0.01[d]
CH-31–99	22	10	*Carthamus lanatus* L. ssp. *baeticus*[a]	22	0	6	13	7	<0.001[e]
CH-2–01	14	12	*Centaurea americana* Nuttall	4	0	2	25	14	0.100
CH-6–01	14	3	*Centaurea americana*	4	1	7[b]	16	11	0.255
CH-7–01	14	4	*Centaurea americana*	5	2	2	6	4	0.567
CH-8–01	14	6	*Centaurea americana*	3	0	5	10	7	0.070
CH-2–02	14	6	*Centaurea americana*	3	0	4	15	10	0.069
CH-20–99	21	5	*Centaurea calcitrapa* L.[a]	48	0	5	38	11	<0.001[e]
CH-1–04	14	6	*Centaurea calcitrapa*[a]	30	0	3	23	22	<0.001[e]
CH-2–04	14	6	*Centaurea calcitrapa*[a]	30	0	4	19	19	<0.001[e]
CH-12–00	14	8	*Centaurea cyanus* L.[a]	30	0	4	12	7	<0.001[e]
CH-14–00	14	10	*Centaurea cyanus*[a]	38	0	6	13	5	<0.001[e]
CH-19–01	14	3	*Centaurea diffusa* Lamarck[a]	34	0	2	19	3	<0.05[c]
CH-10–00	14	5	*Centaurea maculosa* Lamarck[a]	10	0	3	6	4	<0.01[d]
CH-9–01	14	4	*Centaurea melitensis* L.[a]	46	7	2	12	4	0.214
CH-10–01	14	6	*Centaurea melitensis*[a]	51	2	3[b]	24	8	<0.01[d]
CH-15–01	14	6	*Centaurea melitensis*[a]	28	3	1	12	4	0.168
CH-1–00	21	10	*Centaurea sulphurea Willdenow*[a]	12	4	9	10	5	0.666
CH-3–00	21	10	*Centaurea sulphurea*[a]	8	2	6	29	14	0.423
CH-6–00	21	6	*Centaurea sulphurea*[a]	6	0	6	12	8	<0.05[c]
CH-1–99	35	9	*Cirsium brevistylum* Cronquist	6	0	4	9	4	0.103
CH-11–00	14	8	*Cirsium brevistylum*	3	0	7	17	9	0.218
CH-3–01	14	5	*Cirsium hydrophilum* var. vaseyi (A. Gray) J. Howell	6	0	3	11	2	0.515
CH-7–00	14	6	*Cirsium occidentale* var. candidissimum (E. Greene) J. F. Macbride	5	0	2	13	4	0.278
CH-16–00	14	6	*Cirsium occidentale* var. candidissimum	3	0	5	23	8	0.529
CH-5–00	21	3	*Cirsium ochrocentrum* A. Gray[a]	1	0	2	11	2	1.000
CH-17–00	14	4	*Cirsium ochrocentrum*[a]	1	0	2	19	7	1.000
CH-30–99	21	6	*Silybum marianum* L. Gaertner[a]	5	0	5	17	5	0.290
CH-32–99	21	7	*Silybum marianum*[a]	3	0	4	17	8	0.242

[a] Introduced invasive weed.
[b] No female *Ch. succinea* adults survived the test plant portion of the test. Yellow starthistle control data was derived from pooling yellow starthistle control data from each test run before and after the test.
[c] $P < 0.05$, [d] $P < 0.01$, [e] $P < 0.001$; two-tailed *P* value calculated from Fisher's exact test comparing the ratio of infested/noninfested heads of the test against its paired, sequential yellow starthistle control.

Discussion

In 1996, we discovered the unintentional release of the tephritid fly *Ch. succinea* into North America and documented its establishment and rapid spread throughout California (Balciunas and Villegas 1999). We turned our research efforts to studying the safety of this newly arrived natural enemy of yellow starthistle. Overseas scientists had rejected this fly as a potential agent for biological control for yellow starthistle because they felt it posed a risk to safflower (Zwölfer 1972, Sobhian and Zwölfer 1985).

Because many of the plant species we tested in the laboratory were also examined in the field, we can compare our laboratory results to the realized host range. Within the subdiscipline of biological control of weeds, most practitioners feel that laboratory tests can indicate a broader array of hosts than the agent will actually use in the field (Zwölfer and Harris 1971, Schroeder 1983, Wapshere 1989, Cullen 1990). Cullen (1990) notes that laboratory tests help determine the physiological host range—the array of plants on which the agent might potentially feed or develop. Some authors prefer to use the term fundamental host range (Nechols et al. 1992, van Klinken 2000, Sheppard et al. 2005) instead of physiological. The range of plants that the agent actually uses under field conditions is variously referred to as the true host range (Harley and Forno 1992), the ecological host range (Delfosse 1993, Louda et al. 2005), the realized host range (Nechols et al. 1992, Balciunas et al. 1996), or simply as the field host range (van Klinken 2000, Sheppard et al. 2005).

Although we found that *Ch. succinea*, under no-choice conditions in the laboratory, would oviposit and develop on all five varieties of safflower that we tested, we consistently found it at only 1 of the 47 safflower fields that we monitored in California, and there it was only causing minor damage to safflower (Balciunas and Villegas 2001).

A weevil, *Rhinocyllus conicus* (Frölich) (Coleoptera: Curculionidae), released in the western United States in 1969 to control musk thistle, *Carduus nutans* L., raised concerns about the safety of biological control because this weevil also damages native thistles in the genus *Cirsium* (Turner et al. 1987, Louda et al. 1997, Strong 1997). Safflower, yellow starthistle, *Carduus*, and *Cirsium* are all members of the thistle tribe Car-

Table 2. No. heads infested by *Ch. succinea* in each choice test consisting of a test plant species and its simultaneous yellow starthistle control

Test no.	Test plant			Yellow starthistle control		
	Species	Total heads	Heads with *Ch. succinea*	Total heads	Heads with *Ch. succinea*	Fisher exact test two-tailed *P* value
CH-12–01	*Centaurea americana*	7	0	10	1	1.000
CH-20–01	*Centaurea americana*	6	0	27	6	0.563
CH-4–02	*Centaurea americana*	17	1	21	13	<0.001
CH-9–02	*Centaurea americana*	13	1	19	5	0.361
CH-10–02	*Centaurea americana*	14	1	22	14	<0.001
CH-13–01	*Centaurea melitensis*[a]	35	0	17	4	0.009
CH-14–01	*Centaurea melitensis*[a]	50	6	18	1	0.666
CH-5–02	*Centaurea melitensis*[a]	76	1	23	16	<0.001
CH-14–02	*Centaurea melitensis*[a]	50	0	19	17	<0.001
CH-16–01[b]	*Centaurea sulphurea*[a]	9	0	30	18	0.002
CH-17–01	*Centaurea sulphurea*[a]	10	0	14	2	0.493
CH-18–01	*Centaurea sulphurea*[a]	7	1	24	12	0.191
CH-12–02	*Centaurea sulphurea*[a]	17	0	21	5	0.139
CH-15–02	*Centaurea sulphurea*[a]	21	0	14	7	<0.001

[a] Introduced invasive weed.
[b] Four pairs of *Ch. succinea* used in this test rather than six.

dueae, and we were concerned that *Ch. succinea* might also attack the native C*irsium* thistles. However, none of the four native species of C*irsium* that we tested in the laboratory seemed susceptible to attack by *Ch. succinea* (Table 1), nor did we detect any *Chaetorellia* attack on the 19 native and 2 introduced C*irsium* thistles that we collected at our field sites (Table 3). Therefore, we feel that native C*irsium* thistles are unlikely to serve as hosts for *Ch. succinea.* Moreover, our results indicate that any plants in the Cardueae subtribe of Carduinae are probably safe from attack by *Ch. succinea.* In the United States, this subtribe includes not only the native and introduced *Cirsium* spp., and milk thistle (*S. marianum*), but also *Cynara* spp., including commercial artichoke (*Cynara scolymus* L.) (Bremer 1994).

Of the 24 plant species collected in the field, we were able to rear this fly only from yellow starthistle, Malta thistle, and Sicilian thistle. Our laboratory tests correctly predicted that *Ch. succinea* would use both of the latter in the field. American basketflower, *Ce. americana,* is known from 13 states (USDA–NRCS 2006), but, to our knowledge, *Ch. succinea* is not yet established in any of them; therefore, it is too early to confirm its susceptibility to attack by *Ch. succinea* under field conditions.

Our results also confirm the value of no-choice tests. Choice tests are usually accepted as being better predictors of the risk to a given potential host (Zwölfer and Harris 1971, Cullen 1990, Edwards 1999), and for some weed agents, have been the only type of test used (Winder et al. 1984). However, although the infestation rates on *Ce. melitensis* and *Ce. sulfurea* under no-choice conditions were very low, both of these seem to be good alternate hosts in the field.

We were also interested if this fly, like its relative *Ch. australis,* could use other *Centaurea* spp. to extend its breeding season (Turner et al. 1996), or to expand its geographic range into areas where yellow starthistle was not present. Under no-choice conditions, three of the seven *Centaurea* spp., along with the yellow starthistle controls, that we tested in the laboratory were susceptible to attack by *Ch. succinea.* Of the four *Centaurea* spp. we examined in the field, we recovered this fly from yellow starthistle, Malta thistle, and Sicilian thistle. Woods and Popescu (2000) observed infestation by *Ch. succinea* in excess of 20% of the heads of Sicilian thistle at a site in central California. Neither *Ce. rothrockii* nor *Ce. americana* occurs in our region (Keil and Turner 1993), so we were unable to examine field populations of these native *Centaurea* spp. Therefore, we feel there is a definite risk to a few—but not all—members in the subtribe Centaureinae (Bremer 1994), which in the United States includes Russian knapweed (*Acroptilon repens* L. DC), some three dozen *Centaurea* species, and a few species of *Carthamus,* including the important crop, safflower. In the United States, all members of this subtribe, except for two native *Centaurea* species, are introduced, and, except for safflower, they are usually considered undesirable weeds. We tested both the native *Centaurea* spp., *Ce. Americana,* and *Ce. rothrockii* (Kearney and Peebles 1960) and recorded no attack on the latter, but in two of the three tests, there was low oviposition and development on *Ce. americana.*

Chaetorellia succinea is likely to contribute to the eventual control of yellow starthistle in California (Balciunas and Villegas 2001), but we are now concerned about possible impacts by this fly to the native knapweed, *Ce. americana.* Because the range of yellow starthistle includes all but one of the states (Arkansas) from which *Ce. americana* is known (USDA–NRCS 2006), there is a chance that *Ch. succinea* may arrive in these states and attack this attractive native plant. We believe that *Ch. succinea*'s use of *Ce. melitensis* as an alternate host makes attack of *Ce. americana* by this fly even more likely to occur. Texas is one of the few states where *Ce. americana* is relatively common, but yellow starthistle is infrequent there (Correll and Johnston 1979). However, *Ce. melitensis* is fairly common in Texas (Correll and Johnston 1979), as it is in Arizona (Kearney and Peebles 1960). Thus, *Ce.*

Table 3. List of field collections in California and Oregon of Cardueae tribe plants and the percent of heads infested with *Ch. succinea* flies

Species	Date	County	Plants	Seedheads	Percentage of *Ch. succinea* infestation
Centaurea cyanus L.[a]	6/8/99	Shasta	—	188	0
	6/15/99	San Luis Obispo	—	307	0
	7/19/99	Shasta	10	333	0
	8/15/01	Siskiyou	—	548	0
	8/15/01	Siskiyou	—	1,513	0
	8/15/01	Shasta	—	1,053	0
	9/25/01	Plumas	—	1,183	0
	9/26/01	Lassen	—	1,931	0
	9/26/01	Modoc	—	1,857	0
	7/24/02	Kern	—	1,018	0
	7/25/02	Tulare	—	570	0
Centaurea melitensis L.[a]	9/20/99	Amador	30	369	21
	7/9/01	Monterey	21	748	5
	7/24/02	Amador	30	958	6
	7/24/02	Kern	15	528	0
Centaurea solstitialis L.[a]	8/5/98	Humboldt	10	375	48
	8/5/98	Siskiyou	10	316	12
	9/17/98	Napa	—	317	52
	11/2/98	Butte	12	319	46
	7/19/99	Shasta	10	128	16
	7/19/99	Tehama	11	706	44
	9/20/99	Amador	45	1,646	39
	9/20/99	San Joaquin	10	1,000+	70
	10/6/99	Contra Costa	10	300+	61
	11/13/01	San Diego	5	257	0
Centaurea sulphurea Willdenow[a]	7/24/02	Sacramento	245	408	4
Cirsium andersonii (A. Gray) Petrack	7/20/98	Nevada	—	30	0
	8/20/98	Nevada	—	30	0
	8/20/98	Nevada	—	100	0
	8/23/00	El Dorado	—	405	0
Cirsium arvense L. Scopoli[a]	7/20/99	Modoc	11	1,394	0
Cirsium brevistylum Cronquist	7/7/00	Clackamas (OR)	1	15	0
	7/19/00	Linn (OR)	10	221	0
	8/19/00	Del Norte	—	287	0
	8/19/00	Humboldt	—	328	0
	7/9/01	Monterey	10	173	0
Cirsium canovirens Rydberg	7/1/99	Nevada	—	292	0
	7/1/99	Plumas	—	10	0
	7/19/00	Lake (OR)	—	179	0
	8/23/00	Alpine	—	761	0
Cirsium crassicaule (Greene) Jepson	6/15/99	Kern	—	25	0
Cirsium cymosum (Greene) J. T. Howell	8/6/98	Siskiyou	—	319	0
	8/18/98	Lassen	—	138	0
	8/18/98	Lassen	4	40	0
	8/19/98	Modoc	—	293	0
	6/8/99	Siskiyou	—	239	0
	6/8/99	Siskiyou	—	288	0
	7/1/99	Plumas	—	10	0
	7/19/99	Lassen	3	13	0
	7/19/99	Modoc	6	67	0
	7/19/99	Modoc	14	601	0
	7/1/00	Lassen	—	692	0
Cirsium douglasii de Candolle	8/20/98	Nevada	6	—	0
	7/20/99	Modoc	11	526	0
	8/17/00	Humboldt	—	488	0
	8/17/00	Humboldt	—	1,169	0
	8/19/00	Humboldt	—	488	0
	8/29/00	Trinity	—	589	0
	8/29/00	Trinity	—	320	0
	8/30/00	Trinity	—	531	0
Cirsium edule Nuttall	7/15/98	Douglas (OR)	8	—	0
Cirsium loncholepis Petrak	5/27/99	San Luis Obispo	—	105	0
Cirsium occidentale var. californicum (A. Gray) Keil and Turner	5/5/99	Kern	—	60	0
	5/5/99	Kern	—	12	0
	5/26/99	Santa Barbara	—	16	0
	5/26/99	Santa Barbara	—	59	0
	5/26/99	Santa Barbara	8	78	0
	7/13/00	Los Angeles	—	19	0
	7/13/00	Los Angeles	—	85	0

Table 3. Continued

Species	Date	County	Plants	Seedheads	Percentage of *Ch. succinea* infestation
Cirsium occidentale var. candidissimum (Greene) J. F. Macbride	8/4/98	Trinity	5	—	0
	8/7/98	Siskiyou	8	117	0
	8/18/98	Lassen	5	180	0
	8/18/98	Shasta	3	38	0
	8/19/98	Modoc	—	60	0
	9/2/98	Plumas	9	—	0
	9/2/98	Plumas	10	—	0
	9/3/98	Plumas	10	—	0
	7/19/99	Shasta	11	161	0
	7/20/99	Modoc	5	92	0
	7/22/99	Mono	12	291	0
	8/23/00	Alpine	—	122	0
	8/23/00	Alpine	—	56	0
	8/24/00	Mono	8	167	0
	8/29/00	Trinity	—	177	0
Cirsium occidentale var. occidentale (Nuttall) Jepson	7/9/01	Monterey	10	78	0
Cirsium occidentale var. venustum (Greene) Jepson	8/5/98	Humboldt	—	392	0
	6/15/99	Kern	—	138	0
	6/15/99	Monterey	8	95	0
	6/15/99	Monterey	—	63	0
	6/15/99	Fresno	—	150	0
	6/15/99	San Benito	12	277	0
	6/15/99	Fresno	—	113	0
	6/15/99	Fresno	—	150	0
	7/9/01	Monterey	11	52	0
	8/15/00	Mendocino	10	119	0
Cirsium ochrocentrum A. Gray[a]	8/19/98	Modoc	10	114	0
	7/20/99	Modoc	18	121	0
	8/15/00	Lake (OR)	10	44	0
Cirsium quercetorum (A. Gray) Jepson	2000	Monterey	—	177	0
	7/9/01	Monterey	13	45	0
Cirsium remotifolium (Hooker) de Candolle	7/19/00	Linn (OR)	10	96	0
	7/19/00	Linn (OR)	10	102	0
	8/31/00	Curry (OR)	26	112	0
Cirsium scariosum Nuttall	9/2/98	Plumas	4	—	0
Cirsium undulatum (Nuttall) A. Sprengal[a]	7/12/98	Wheeler (OR)	6	32	0
	7/19/00	Lake (OR)	10	—	0
Cirsium vulgare (Savi) Tenore[a]	7/16/98	Siskiyou	10	298	0
	8/5/98	Humboldt	12	346	0
	8/18/98	Shasta	—	149	0
	7/20/99	Modoc	5	149	0
Cnicus benedictus L.[a]	7/9/01	Monterey	23	91	0

[a] Introduced invasive weed.

melitensis may serve as a bridge or stepping-stone host, allowing *Ch. succinea* to more easily reach the populations of *Ce. americana* in the southwest from which it is now isolated by the absence of its primary host, yellow starthistle.

To better predict the geographic range and impact of future agents, we would recommend the inclusion of more weedy species in their host range evaluations of potential weed biological control agents. Currently, native species and commercial crops receive the most emphasis. The possibility of another weed serving as an alternate host, and thereby expanding the geographical distribution of the agent, is usually not considered. For example, before the release of *Chaetorellia australis*, in addition to yellow starthistle, only three other species of *Centaurea* were tested (Turner et al. 1990). Of these three, the only weed, *Ce. cyanus*, was a good alternate host for the fly, but this was viewed as helpful for its establishment (Turner et al. 1996). However, *Ce. cyanus* occurs at many sites, especially at higher elevations, where yellow starthistle is not found. *Ch. australis* has become common at some of these areas where yellow starthistle is absent, and obviously, is not contributing to its control.

We would also recommend monitoring yellow starthistle, *Ce. melitensis*, and *Ce. americana* populations in Arizona, New Mexico, and Texas for signs of attack by *Ch. succinea*. Little is known about the field biology and ecology of this fly (e.g., adult longevity, number of generations per year), and these need study as well. The factors that increase or limit this fly's impact on yellow starthistle, including the presence/absence of other biological control agents, should also be studied.

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